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HISTORICAL ECOLOGY: USING UNCONVENTIONAL DATA SOURCES TO TEST FOR EFFECTS OF GLOBAL ENVIRONMENTAL CHANGE¹

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Predicting the future ecological impact of global change drivers requires understanding how these same drivers have acted in the past to produce the plant populations and communities we see today. Historical ecological data sources have made contributions of central importance to global change biology, but remain outside the toolkit of most ecologists. Here we review the strengths and weaknesses of four unconventional sources of historical ecological data: land survey records, “legacy” vegetation data, historical maps and photographs, and herbarium specimens. We discuss recent contributions made using these data sources to understanding the impacts of habitat disturbance and climate change on plant populations and communities, and the duration of extinction–colonization time lags in response to landscape change. Historical data frequently support inferences made using conventional ecological studies (e.g., increases in warm-adapted species as temperature rises), but there are cases when the addition of different data sources leads to different conclusions (e.g., temporal vegetation change not as predicted by chronosequence studies). The explicit combination of historical and contemporary data sources is an especially powerful approach for unraveling long-term consequences of multiple drivers of global change. Despite the limitations of historical data, which include spotty and potentially biased spatial and temporal coverage, they often represent the only means of characterizing ecological phenomena in the past and have proven indispensable for characterizing the nature, magnitude, and generality of global change impacts on plant populations and communities.

Key words: climate change; colonization; extinction debt; habitat fragmentation; herbarium specimens; historical ecology; land surveys; maps; repeat photography; time lags.

Many ecological phenomena are impossible to fully understand without considering processes acting over preceding decades, centuries, or longer. A dominant tree species may owe its abundance to favorable conditions for recruitment that occurred during a brief window of time decades ago, but never since (e.g., Gedalof et al., 2006). An unusually high density of nutrient-demanding plants may be the result of agricultural soil amendments that ended centuries ago (e.g., Dupouey et al., 2002). The absence of shade-tolerant plant species from a site that is suitable for population establishment may be explained by extinctions due to a singular disturbance event, and a protracted process of recolonization given severe spatial constraints on seed dispersal (Flinn and Vellend, 2005). Global biological change is thus not only a contemporary phenomenon, but a historical one as well.

Over the past 20 yr, compelling arguments have been made for the importance of incorporating historical perspectives into ecological studies to understand the structure and function of present-day ecosystems and to evaluate different conservation

goals (Swetnam et al., 1999; Foster, 2000; Egan and Howell, 2001; Jackson and Hobbs, 2009). Historical land surveys, aerial photographs, maps, and herbarium specimens (among other data sources) have been increasingly incorporated into “mainstream” research in ecology and conservation. Historical approaches have been especially influential in restoration ecology, given the explicit goal in restoring a degraded ecosystem to some past and more desirable state (Egan and Howell, 2001). In North America, for example, the use of ecosystem states immediately before European settlement as benchmarks for conservation and restoration has been challenged by historical data indicating both a profound influence of native peoples on presettlement ecosystems and the constant biotic change due to both natural and anthropogenic factors during the preceding centuries (Foster, 2000; Bjorkman and Vellend, 2010).

Previous reviews of historical ecology have emphasized the need for a long-term view to understand present-day patterns, with a specific focus on establishing more realistic and defensible goals for ecosystem management (Swetnam et al., 1999; Foster, 2000; Egan and Howell, 2001; Jackson and Hobbs, 2009; Szabó, 2010). At the same time, from one point of view, appeals to historical explanations for ecological phenomena—specific to a particular place—do not advance the goal of elucidating general explanations for patterns in nature (Kingsland, 1995). However, we maintain that historical approaches simply provide a means of extending the time frame for ecological studies, rather than a pursuit of qualitatively distinct kinds of explanation, and therefore, a variety of historical methods can be applied to fundamental ecological questions. This is not

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a new perspective, but the last decade in particular has seen a proliferation of studies applying historical methods to fundamental questions concerning the responses of plant populations and communities to environmental change.

In this paper, we provide an overview of historical ecological data sources that one might consider unconventional, in the sense that they are not in the arsenal of methods used by the typical ecologist. Using previous reviews and perspectives as a point of departure, we then highlight studies using historical methods to address two fundamental issues in global change biology that have been especially prominent over the past decade: (1) The influence of dominant global change drivers—climate warming and land-use change especially—on temporal change over decadal scales in plant communities, and (2) extended time lags in the response of plant populations and communities to environmental change (anthropogenic or otherwise).

HISTORICAL ECOLOGY: DEFINITIONS AND SCOPE

The term “historical ecology” has been adopted by two main groups of researchers: biologists drawing on historical methods and explanations for ecological phenomena, which may or may not involve anthropogenic factors, and social scientists drawing on ecological principles to better understand human history (Szabó, 2010). Our review focuses on the first group, although we note that the two groups frequently share overlapping goals. The topic of historical ecology can potentially include a vast range of methods and time scales, so to minimize redundancy with previous treatments, we restrict our focus in several respects. First, we focus on unconventional methods (admittedly a subjective judgment), thereby excluding full-fledged subdisciplines of ecology such as paleo- and dendroecology, both of which fall under the umbrella of historical ecology (Swetnam et al., 1999). Second, we focus on studies that draw on evidence that was not itself amassed for the purposes of long-term ecological study, thereby excluding from consideration continuous long-term studies. Finally, we focus our examples largely on methods allowing quantification of one or more ecological variables—e.g., habitat types, community composition, phenology—and less on methods allowing only qualitative assessments (e.g., oral history, historical written descriptions).

METHODS IN HISTORICAL ECOLOGY

Historical ecology is a necessarily opportunistic science: we cannot travel backward in time, so we must make use of whatever sources of historical data are available. Here we highlight the four main sources of data that fall within our criteria of unconventional and quantitative (see above) and that have made especially important contributions to understanding global change: historical landscape and vegetation surveys, historical maps, historical photographs, and herbarium records. Here we provide a brief overview of each of these data sources, including strengths and weaknesses specific to each method (Table 1). A more detailed treatment of historical ecological methods, including data sources, can be found in Egan and Howell (2001). A strength that applies to all such data sources is that they often provide the only empirical means of estimating an ecological variable of interest (e.g., species composition, flowering time) at particular times in the past. A common limitation is that temporal

coverage is typically spotty, often with just one or two snapshots of the past with which to compare the present.

Historical surveys of landscapes and vegetation—Historical surveys of landscapes and vegetation are treasure troves of information about the diversity and composition of plant communities in the past. This category includes land surveys carried out by Europeans in North America and other parts of the New World just before or during the process of settlement, and vegetation surveys carried out by ecologists over the last century or so (“legacy studies”).

Land surveys—During the settlement of North America and other regions by Europeans in the 17th–19th centuries, governments commissioned land surveys to delineate property boundaries and identify areas for agriculture, forestry, or mining (Whitney and DeCant, 2005). The earliest surveys used variable methods, but by the mid-1800s many surveys were carried out according to stricter standards such as those of the General Land Office of the United States (Whitney and DeCant, 2005). Surveyors walked straight lines across the land, noting vegetation and topography. At each posted grid corner, the species identity, diameter, and distance-to-post of one to several “bearing” or “witness” trees were recorded (Fig. 1A). Trees that intersected survey lines (“line trees”) were also noted. The great advantage of land surveys is the detail they provide on vegetation across large areas (Schulte and Mladenoff, 2001; Table 1), allowing reconstruction of forest composition and density just prior to the sweeping changes brought by settlement, deforestation, agriculture, and the cessation of First Nations land management (McIntosh, 1962; Cogbill et al., 2002; Foster et al., 2004).

Land survey records have some important limitations (Schulte and Mladenoff, 2001; Table 1). For example, the selection of bearing trees may have been biased toward certain species or larger trees, although the degree of this potential bias can be estimated by comparing data for bearing trees and line trees, as the latter were not selected by any criteria other than intersecting the line (Bjorkman and Vellend, 2010). There also may be inconsistencies in species identification by different surveyors, although comparisons within and across different surveyors and locales has shown a remarkable accuracy and consistency in tree identification (Whitney and DeCant, 2005). While these limitations force us to interpret data cautiously, they are far outweighed by the uniqueness and utility of information provided (Liu et al., 2011).

Legacy studies—Ecologists have been quantitatively surveying vegetation for more than a century. If the legacy of data they left behind is accessible, spatially referenced, and with well-documented methods (Fig. 1B), contemporary resurveys permit assessment of plant community changes over the intervening decades. The time scale covered by such studies (up to a century) falls in between those covered by paleoecology (millennia) and by short-term ecological studies (a few years), thus providing a crucial baseline for changes within a century that would otherwise not be available. Recent studies have used legacy data collected by well-known ecologists like J. T. Curtis in Wisconsin (Rogers et al., 2009), R. H. Whittaker in Oregon (Damschen et al., 2010), and Ronald Good in England (Keith et al., 2009). The spatial scale of legacy data varies from a single, small, protected area to entire countries, with some legacy data resulting from coordinated state or national efforts to survey vegetation

TABLE 1. Key advantages and limitations of methods in historical ecology.

Method	Advantages	Limitations	Solutions (to overcoming limitations)
Land surveys	Broad spatial coverage	Possible biases in selection of bearing trees	Comparison with “line trees” or other independent data
	Time period of particular interest: just before European settlement	Uncertain reliability of tree identification	Use coarse taxonomic resolution
	Allows quantitative comparisons with present conditions	Data limited to trees and habitat types	
Legacy studies	Detailed, local-scale community composition data	Plots often not permanently marked	Base inferences on groups of plots rather than individual plots
	Decadal time scales, not covered by most other data sources	Limited spatial coverage (haphazard availability)	Survey multiple contemporary plots for each historical plot
		Outdated/uncertain taxonomy	Use coarse taxonomic resolution
Historical maps	Landscape-scale coverage	Uncertain spatial accuracy	Verification using independent data (e.g., written records)
	Covers prephotography time period	Uncertain correspondence of historical and contemporary land cover types	Lumping fine-scale land cover classes
Historical photos	Broad spatial coverage	Coarse characterization of vegetation (e.g., woody vs. herbaceous)	Verification using independent data (e.g., field observations)
	Often available for multiple time periods (e.g., every 10–20 yr)	Low image quality	Image enhancement (e.g., edge detection)
		Uncertain angle, locations, or dates	Exclusion of images/variables overly sensitive to yearly timing
Herbarium records	Global spatial coverage	Geographic collection biases	Use of independent data to quantify and correct for bias
	100+ years temporal coverage	Temporal variation in collection frequency	Assess robustness of conclusions by using repeated subsets of data
	Rich in information: species presence, phenology, traits	Low sample size (at given place and time)	Group collections across larger spatial areas and time periods
		Possible uncertainty in spatial location	Limit analyses to species with good spatial/ temporal coverage

(e.g., Boggess and Bailey, 1964; Chytrý and Danihelka, 1993; Franklin et al., 2004).

The use of legacy data in a resurvey study presents several challenges, largely related to the fact that studies in the past were often not designed with resurveying in mind: plots were not always permanently marked, with location descriptions of variable utility (Fig. 1B). Differences in the location of plots

can lead to “pseudoturnover”, in which extinction and colonization are overestimated (Nilsson and Nilsson, 1985). When there is uncertainty in plot relocation, rather than drawing inferences about individual plots, inferences are typically drawn at the level of groups of plots (often 20 or more), at which level pseudoturnover should represent only a minor source of random variation relative to systematic changes over time (e.g., Rogers et al., 2009;

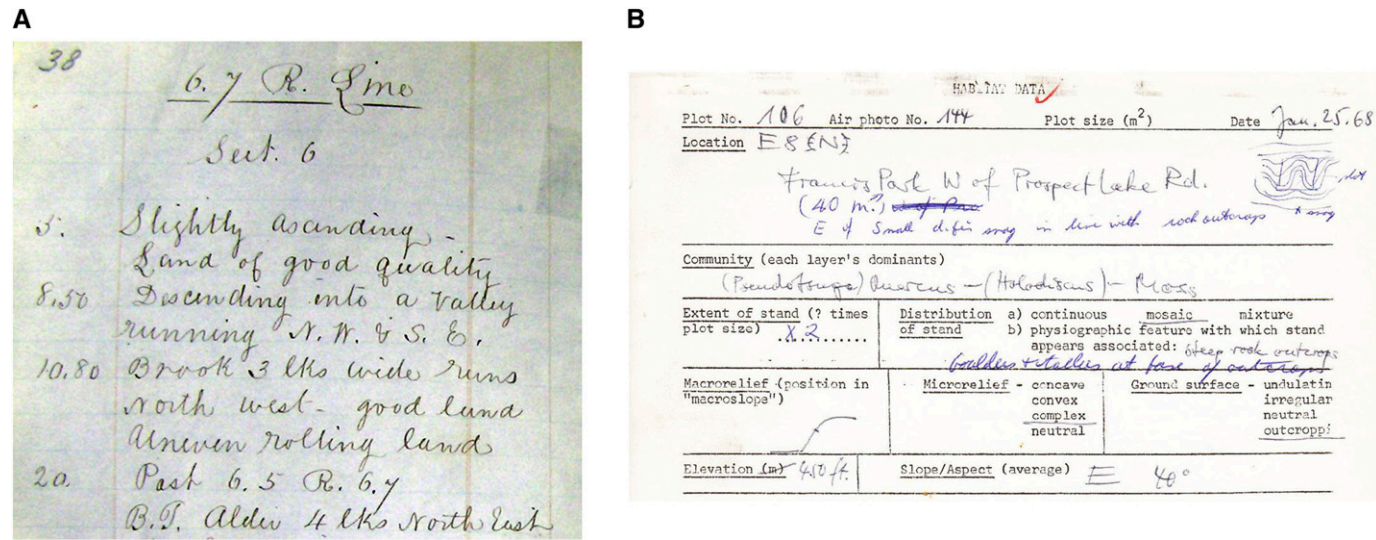


Fig. 1. (A) Surveyor notes from 1859 in the Shawnigan District of Vancouver Island, British Columbia, Canada, describing the survey line running north-south between ranges 6 and 7 in section 6 (an east-west unit of space). An alder was marked as a bearing tree (“B.T.”) 4 links (~20 cm/link) from the corner post (Bjorkman and Vellend, 2010). (B) Field notes from a legacy vegetation study by Roemer (1972) on Vancouver Island, where resurveys were conducted in 2009 (J. McCune, unpublished data). Site 106 was relocated in the field using the information on slope, elevation, and other topographic features, as well as the “Location” description, which included a grid cell designation (“E8”) plus quadrant of this grid cell (“N”) on a custom-gridded aerial photograph (“144”), which was available from the original author.

Damschen et al., 2010). Resurveys of legacy plots must also deal with changes over time in nomenclature and in the taxonomic resolution used by different observers (Table 1). Several online tools have been developed to match synonymous species names (e.g., <http://www.tropicos.org>, <http://www.ipni.org>, <http://www.itis.gov>).

Historical maps—Historical maps are an invaluable source of land-cover information, particularly for prephotography time periods. While historical maps do not typically contain information on local plant community composition, the delineation of past land uses (e.g., crops or pastures) and natural habitats (e.g., wetlands, forests)—in exceptional cases, going back as far as 700+ years—can provide unique opportunities for investigating the imprint of landscape history on present-day vegetation (e.g., Verheyen et al., 1999; Cousins, 2001; Cousins and Eriksson, 2001; Fig. 2).

Historical maps were produced for a variety of reasons, including delimiting property boundaries, land use planning, military planning, or industries such as the fur trade (Reithmaier, 2001; Giordano and Nolan, 2007; Ruggles, 2011). Variation in the experience, intent, and political, economic, or other predispositions of a given cartographer present challenges to the use of maps in ecological research (Swetnam et al., 1999). Maps produced for some purposes, such as military planning (Fig. 2), are unlikely to contain systematic biases and have been used “as is” in many ecological studies (e.g., Verheyen et al., 1999; Cousins,

2001). In cases of uncertain land cover classification or spatial delimitations, verification using independent data sources, such as aerial photographs, historical texts, censuses, or present-day field evidence of historical land use is necessary before using historical maps in ecological studies (Reithmaier, 2001). Errors or uncertainties in historic land cover classifications can also be minimized by lumping relatively fine distinctions into broader categories, such as managed vs. unmanaged grasslands (e.g., Cousins, 2001; Cousins and Eriksson, 2001).

Historical photos—Repeat photography is a powerful tool for assessing temporal ecological change. Photographs have been used to track biophysical changes such as glacial retreat or advance and soil erosion (Cerny, 2010), as well as vegetation changes, including tree line shifts (Danby and Hik, 2007; Harsch et al., 2009), shrub expansion in tundra, savanna, and grassland ecosystems (Tape et al., 2006; Maestre et al., 2009; Wigley et al., 2010), and forest cover changes in agricultural landscapes (Fig. 3).

Repeat photographs are of three types: aerial (directly downward from an aircraft), oblique (downward on an angle), and ground-based. Photographs vary in spatial extent and detail and can therefore each contribute complementary insights into vegetation change. For example, in tree line and tundra ecosystems, aerial photography has been used to quantify change in cover of conspicuous species such as trees or large shrubs at the landscape scale (e.g., Danby and Hik, 2007), oblique photography



Fig. 2. A historical “Ferraris” land cover map produced for military purposes ~1775 showing one section of the Vlaams-Braabant region of Belgium, which was one of two landscapes used to test for an extinction debt among forest plants (Vellend et al., 2006). The light areas shaded with straight lines represent agriculture; dark green with dots (trees) represents forest; green areas without dots represent wet meadow/grassland (K. Verheyen, Ghent University, personal communication). Reproduced with permission (Institut géographique national—A2753, <http://www.ngi.be/FR/FR1-4-2-3.shtm>).

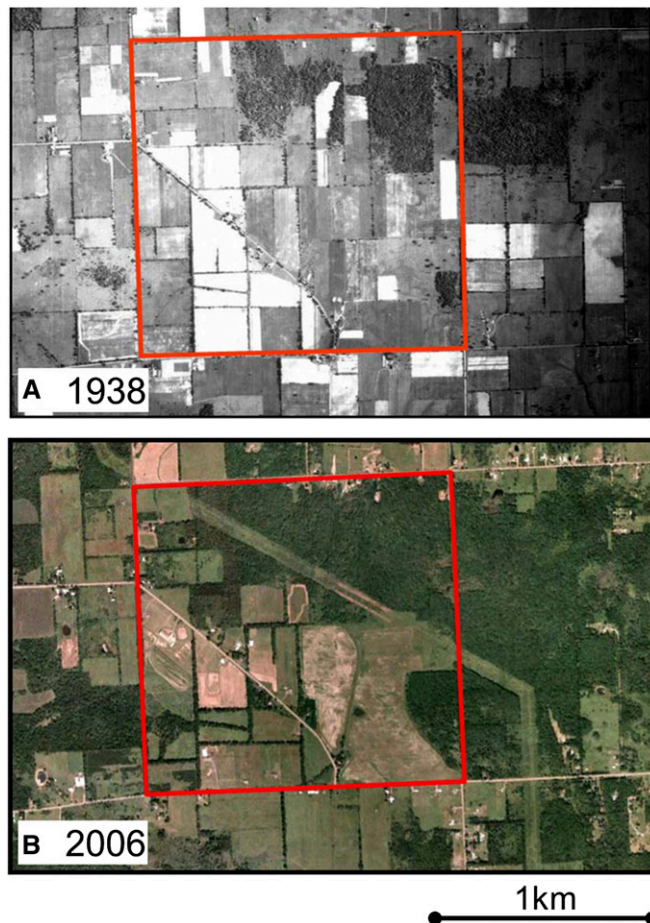


Fig. 3. Historical and contemporary aerial photographs used to reconstruct forest history in Tompkins County, New York (Smith et al., 1993). The red square delimits the same area in the two photos.

has been used to characterize shrub patch dynamics across hill slopes (e.g., Tape et al., 2006), and ground-based photography has been used to identify changes to individual willow patches (e.g., Myers-Smith et al., 2011).

Repeat photography has limitations that include low image quality of early photographs, photo angle geometry that can limit quantification of observed patterns, uncertain locations shown in original photographs, and unknown date or time of image collection that could result in diurnal or seasonal variation between photo comparisons (Pickard, 2002; Table 1). Some of these limitations can be addressed by image enhancement including edge detection, corrections such as orthorectification, incorporating additional information from historical records, and limiting the photographic analysis and interpretation to vegetation that undergoes less phenological change (Pickard, 2002; Morgan et al., 2010). Improved techniques are currently being developed for quantitative photographic analysis, including methods of image enhancement and automated pixel or object-based image classification (Morgan et al., 2010).

Herbarium specimens—Herbarium specimens—with information on the place and time of collection—can be used to generate historical data on the geographic distribution, phenology, nutrient content, and genetics of plants (Primack and Miller-Rushing, 2009). Hundreds of thousands of herbarium specimens have been

collected around the world over the past 100+ years, thus providing data for a huge number of species, across large spatial and temporal scales, and in locales where other data may be sparse (Primack and Miller-Rushing, 2009). Herbarium collections have been used to assess the spread of invasive plants (e.g., Delisle et al., 2003), temporal trends in abundance (e.g., Hedenäs et al., 2002), and temporal changes in morphological traits such as height or leaf properties (e.g., Buswell et al., 2011). Of particular interest here, the study of plant phenology has been greatly facilitated by herbarium collections, through studies of the abiotic (e.g., climatic) cues of phenological events such as flowering (Rivera and Borchert, 2001; see Fig. 4).

The greatest challenge in using data from herbarium specimens to address ecological questions stems from geographic and temporal collection biases. Herbarium specimens are generally not collected at random or regular spatial locations, but instead tend to be concentrated around areas of easy access or special interest (Loiselle et al., 2008). There is also substantial temporal variation in collection frequency (Feeley and Silman, 2011). To account for such biases, researchers typically seek independent information to first quantify the bias and then to correct for it (Table 1). For example, in studies focused on potential temporal changes in the abundance of particular focal species, temporal variation in collection frequency can be estimated and corrected by using a large sample of specimens of nonfocal species known to have relatively stable abundances over time (e.g., Hedenäs et al., 2002; Delisle et al., 2003). Despite the limitations, recent work has indicated that herbarium records produce similar estimates of long-term phenological changes to those produced by in-situ observation (e.g., Miller-Rushing et al., 2006; Robbirt et al., 2011).

APPLICATION 1: PLANT RESPONSES TO GLOBAL CHANGE

In this section, we present an overview of studies quantifying temporal change in plant populations and communities, in which some attempt was made to infer the underlying global change drivers. We focus on habitat destruction, disturbance regimes, and climate as key drivers of change, with additional examples summarized in Table 2.

Habitat destruction, fragmentation, and disturbance—Human land use has impacts that vary widely in magnitude, from relatively minimal extraction of forest resources to the wholesale replacement of natural vegetation with agriculture or urban development. Historical data have allowed ecologists to characterize the impacts of a wide range of different changes in land use.

Wholesale habitat loss has been quantified by comparing land survey data with contemporary land cover, revealing that habitat loss via land conversion to agriculture has been especially drastic for plant communities occupying deep, fertile soils. For example, compared to the time prior to European settlement (150+ years ago), less than 10% of the oak savannas of Vancouver Island (Vellend et al., 2008), 1% of *Imperata cylindrica* (L.) P. Beauv.-dominated wet tropical grasslands in North Queensland, Australia (Kemp et al., 2007), and a mere 0.02% of the oak savanna of the American Midwest remain today (Nuzzo, 1986). In addition, remnant communities are found in an extremely biased subset of the historic range of edaphic and topographic conditions. Oak savannas on southern Vancouver Island, for

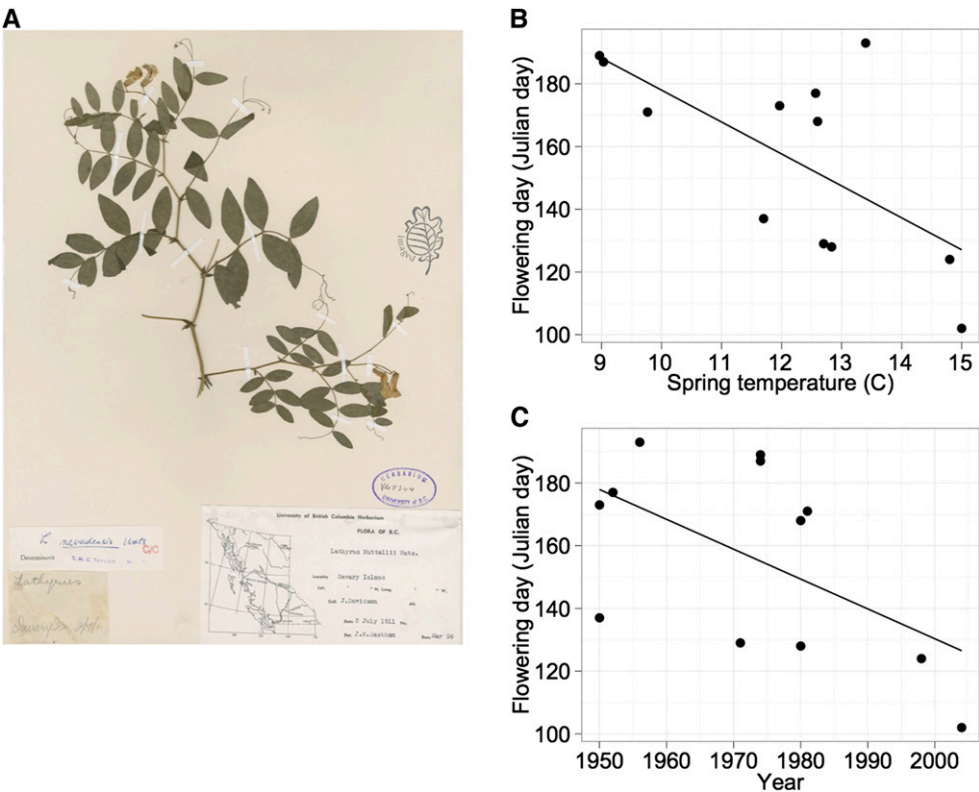


Fig. 4. An example of the use of herbarium specimens to detect phenological responses to recent climate change, from a study of ~40 species in British Columbia, Canada (H. M. Kharouba, unpublished data). (A) A herbarium specimen of *Lathyrus nevadensis* S. Watson collected on Savary Island, British Columbia (49.9°N, 124.8°W). (B) Relationship of flowering date in *L. nevadensis* to mean spring temperature (likelihood ratio $\chi^2_{4,3} = 6.91$, $p = 0.0086$; mixed model with location as a random effect). (C) Change in flowering date over time (likelihood ratio test $\chi^2_{4,3} = 4.46$, $p = 0.0347$; mixed model with location as a random effect).

example, once occurred dominantly on flat, low-elevation deep-soil sites, but now occur almost exclusively in steep, shallow-soiled, high-elevation refugia (Vellend et al., 2008). This bias is one of the reasons remnants of “old-growth” vegetation are often not reliable representatives of presettlement conditions (Cogbill et al., 2002).

Historical data have also been used to test the island-biogeographic prediction that extinction rates should be highest

TABLE 2. Examples of different historical data sources being used to draw inferences concerning links between global change drivers and responses in plant populations and communities.

Global change driver	Historical data	Time span (yr)	Response variable(s)	Results	Example
Habitat loss	Land surveys	~150	Habitat area, habitat-environment relationship	Massive decline in habitat; remnant patches confined to poor, shallow soils	Vellend et al. (2008)
Fire suppression	Land surveys	~150	Tree composition, forest density	Increase in fire-sensitive species; increased tree density	Bjorkman and Vellend (2010)
Land use change	Historical maps	~700	Area of habitat types (e.g., forest, arable land)	Huge fluctuations in land cover (e.g., 0–90% forest at different times)	Verheyen et al. (1999)
N deposition + soil acidification	Legacy data	~40	Community composition	Increase in N indicator species	Van Calster et al. (2007)
Increased deer populations	Legacy data	~50	Community composition	Native species declines most pronounced in areas with no hunting	Rooney et al. (2004)
Climate change	Repeat photography	~40	Range expansion	Increased canopy size and tree density; upslope shift in treeline	Danby and Hik (2007)
Climate change	Legacy data	~60	Community composition	Decreased abundance of cold-adapted species	Harrison et al. (2010)
Climate change	Herbarium specimens + photos	~150	Flowering time	Advanced dates of flowering	Miller-Rushing et al. (2006)

in the smallest remnant habitat patches, and that landscape structure (patch size and connectivity) should be an increasingly dominant driver of community diversity in fragmented landscapes. Using legacy data in Wisconsin prairies, Leach and Givnish (1996) found that indeed more species were lost from smaller than larger fragments over 30–50 yr. The same response was observed for upland woodland fragments in Wisconsin (Rogers et al., 2009), where a weakening of vegetation–environment relationships over time was also found: plant communities whose composition was once linked strongly to soil texture and nutrients are now more strongly influenced by the forest fragment size and spatial context (Rogers et al., 2008). Finally, several studies using legacy data have found evidence of biotic homogenization, whereby a few disturbance tolerant species become widespread, leading to a decline in beta diversity (e.g., Rooney et al., 2004; Keith et al., 2009).

Land-use changes involve more than just conversion of natural vegetation to human uses such as agriculture. In the Americas, Australia, and elsewhere, European settlement resulted in an abrupt shift from traditional indigenous management practices to European ones, with one major consequence being a change in fire regimes from frequent, low-intensity, prescribed burns to fire suppression by European settlers (Vale, 2002). A resurvey of bearing trees on southeastern Vancouver Island (Fig. 1A) revealed a doubling in forest density since European settlement (mid-19th century), accompanied by an increase in fire-sensitive tree species and a shift in the tree size-class distribution toward a higher proportion of smaller trees (Bjorkman and Vellend, 2010). Legacy studies have revealed the effects of continuing fire suppression during the 20th century. In the San Bernardino Mountains of California, for example, Minnich et al. (1995) found a 77% increase in forest density in stands that had not burned since the first survey of plots in the 1930s, which was shortly after fire suppression began.

Climate-driven change in plant communities—Climate change is pervasive across the globe and is thus the dominant topic in the field of global change biology. Based on first principles, predictions include range shifts toward higher latitudes and elevations, decreased local abundance of relatively cold-adapted species (and vice versa), and advances in the timing of key phenological events such as flowering. Historical data of many types have played a central role in testing these predictions over long time scales.

Studies of treeline shifts have been greatly advanced using repeat aerial photography, given the clear distinction of trees from other types of vegetation in photographs. In a meta-analysis of treeline shifts (Harsch et al., 2009), 21 of the 166 sites evaluated used historic aerial or ground photos to determine past treeline position: half of the treelines examined had advanced in the past 100 yr, and treeline advance was more likely where winter warming was most pronounced. Historical photographs are frequently combined with dendrochronology and contemporary demographic surveys to document changes in treeline or in elevational shifts of particular species (e.g., Danby and Hik, 2007; Beckage et al., 2008).

For plant species not directly visible in photographs (e.g., most herbs), legacy data has been critical to assessments of temporal vegetation change. In alpine areas of Europe, legacy data has revealed that species richness has often increased on alpine summits, and species' distributions have shifted upward in elevation, particularly on lower elevation summits

where the pool of species with the potential for upward range shifts is larger (Stöckli et al., 2011). In the Siskiyou Mountains of Oregon, Harrison et al. (2010) resurveyed areas originally surveyed in ~1950, finding compositional changes at low elevations consistent with a warmer and drier climate, in particular, decreased relative abundance of cold-adapted species.

For tropical ecosystems, home to most of the Earth's plant diversity, usable photographs and legacy data are rare or absent for most regions, and even contemporary data on species distributions and diversity are not nearly as abundant as for other ecosystems (Feeley and Silman, 2011). Tropical ecologists have recently begun to fill this void by using location data on herbarium collection records (e.g., Feeley and Silman, 2010). Feeley and colleagues (Feeley and Silman, 2010; Feeley, 2012) used data from herbarium specimens to document shifts in thermal distributions of tropical plant species, with results largely consistent with predictions based on warming temperatures. However, given substantial variation among species, it remains difficult to predict how many tropical plant species are likely to expand into newly climatically suitable habitats or to tolerate rising temperatures (Feeley, 2012).

The study of phenology, a major thrust of climate change research, has been greatly advanced using historical data sources (Fig. 4). Long time series are needed to maximize the strength of inferences concerning climate-phenology links and to test for temporal trends in the face of considerable interannual variability (Robbirt et al., 2011; and Iler et al., 2013, and Wolkovich et al., 2013 in this issue). Herbarium records and other unconventional data sources have extended the temporal depth of phenological studies to a century or more. For example, in New England, a combination of herbarium records and photographs dating to the early 1900s revealed advances in the date of woody-plant flowering, consistent with warming temperatures (Miller-Rushing et al., 2006). In Kyoto, Japan, Aono and Kazui (2008) reconstructed spring temperatures between the years 801 and 2005 using data on cherry flowering from old diaries, advertisements, and poetry. Other sources of phenological data include legacy data from amateur naturalists and naturalist societies as well as agricultural records (Sadras and Monzon, 2006; Carroll et al., 2009).

The studies described thus far focused largely on testing whether ecological changes over time were consistent with expectations based on particular drivers of global change. Historical methods have clearly provided a massive amount of evidence that habitat fragmentation and climate change (among other global change drivers) have had major ecological impacts over the long term. However, in many cases, the full extent of impacts may, in fact, be underestimated if there are extended time lags between an environmental change (e.g., an increase of 1°C or a reduction of habitat area) and the full manifestation of ecological responses.

APPLICATION 2: EXTINCTION DEBTS AND COLONIZATION CREDITS

Time lags between environmental change and colonization–extinction responses have been the focus of a flurry of recent studies using historical methods (Lindborg and Eriksson, 2004; Helm et al., 2006; Vellend et al., 2006; Kuussaari et al., 2009; Bennett et al., 2013). When a local environment changes, some

species are expected to increase in abundance or to colonize from elsewhere, at the same time that other species are expected to decline in abundance, possibly to the point of extinction (Jackson and Sax, 2010). If the underlying process rates are relatively slow, due to factors such as severe habitat fragmentation (low colonization rate) or individual longevity (slow declines to extinction), communities may remain in transient states for many decades or even centuries.

In the case of species richness and turnover dynamics, two kinds of time lags are involved. An “extinction debt” refers to the local presence of species on a deterministic decline toward extinction (Tilman et al., 1994), while a “colonization credit” refers to the absence of species for which colonization is inevitable given that local conditions are suitable for colonization and their presence elsewhere in the landscape (Piqueray et al., 2011). Given the ubiquity of environmental changes, evaluating the magnitude and duration of such debts and credits is critical to a fundamental understanding of present-day community properties and the conservation value of different sites (Jackson and Sax, 2010).

Extinction debts—A number of tests for time lags in response to landscape change were only made possible by historical reconstructions of landscape structure, using some combination of historical maps and photographs created decades or centuries ago (Flinn and Vellend, 2005; Kuussaari et al., 2009; Fig. 2). In landscapes with a recent history of habitat loss and fragmentation, when landscape context (i.e., patch connectivity, area) in the past is a better predictor of present-day species richness than present landscape context, authors have inferred that patch-level diversity has yet to decline to its new equilibrium, that is, that there is an extinction debt. For example, Lindborg and Eriksson (2004) found that plant species richness in seminatural grassland patches in Sweden was predicted by connectivity 50–100 yr earlier but not by present-day connectivity. Helm et al. (2006) found similar results for grasslands in Estonia, and further used patches with historically stable area to estimate an extinction debt of roughly 40% for patches recently reduced in area. By comparing individual species’ responses to forest patch area, connectivity and habitat quality in two landscapes—one with roughly constant forest cover of ~5–8% in recent centuries (Lincolnshire, UK), the other with a pre-1900 decline in forest cover from 25 to 6.5% (Vlaams-Brabant, Belgium, Fig. 2)—Vellend et al. (2006) identified a particular suite of species that contributed most to extinction debt. Species with large, poorly dispersed seeds and long lifespans were independently found to have low rates of colonization and extinction (Verheyen et al., 2004), and only these species were found to contribute to an extinction debt in Vlaams-Brabant (Vellend et al., 2006). Other studies have also found evidence suggestive of extinction debts in temperate plant communities (reviewed in Kuussaari et al., 2009), although there are cases in which historical landscape structure does not improve predictions of present-day diversity patterns beyond those made based on current landscape structure (Cousins, 2009).

Colonization credits—The term “colonization credit” (Piqueray et al., 2011) and its synonyms “immigration credit” (Jackson and Sax, 2010) and “invasion debt” (Bennett et al., 2013) are more recent additions to the literature, although studies of the phenomenon pre-date the development of the terminology. In many studies of temperate forests in which ages of postagricultural stands were established using historical photos and

maps (Figs. 2, 3), species richness of understory plants increased as a function of stand age, with the greatest richness found in primary or ancient forests (reviewed by Flinn and Vellend, 2005). An important role for limited dispersal, and thus the prolonged existence of a colonization credit, has been established via introduction experiments that confirm habitat suitability of postagricultural forests (Flinn and Vellend, 2005). Time lags of decades between the creation of suitable habitat and colonization of plant species have been found in other systems using similar methods (e.g., Piqueray et al., 2011). In Box 1, we use a simple model illustrate the importance of such enduring extinction and colonization time lags for ecology and conservation.

DISCUSSION

Lessons from historical ecological studies: Overview—In this paper, we have highlighted a relatively small proportion of historical ecological studies addressing fundamental ecological issues. It is clear that such studies have contributed profoundly to our understanding of long-term patterns and processes of change in plant populations and communities.

In many instances, historical studies provide independent tests of important ecological questions, supporting results from studies using conventional methods. For example, short-term experiments manipulating variables such as climate or herbivory have revealed responses such as increased shrub cover in the arctic with warming (Elmendorf et al., 2012) or declines in palatable plant species in the presence of herbivores (e.g., Horsley et al., 2003). Longer-term temporal trends revealed by historical studies are often consistent with such hypothesized drivers of vegetation change (e.g., Rooney et al., 2004; Wigley et al., 2010).

Historical studies often provide insights that could not have been generated in any other way. A particularly striking example is the influence of indigenous people’s use of fire prior to European settlement, for which land survey data and paleoecological data provide the only means of characterizing plant communities in the key presettlement time period (e.g., Bjorkman and Vellend, 2010). Many assessments of extinction debts that might last for decades or centuries have also been entirely reliant on historical data from maps or photographs (e.g., Helm et al., 2006; Vellend et al., 2006).

Interestingly, there is not always agreement between historical and contemporary studies on the magnitude of effects of global change drivers. For example, Wolkovich et al. (2012) found far greater sensitivity of flowering phenology to temperature using long-term records (including historical data) than using data from experimental temperature manipulations. Baeten et al. (2010) combined predictions of temporal forest vegetation change based on a chronosequence study (composition of recent forests should converge with that of primary forests) with a survey of 30-yr-old legacy plots. Surprisingly, there was no such convergence, with the magnitude of compositional change just as great in ancient as recent forests (Baeten et al., 2010), indicating that chronosequences may fail to predict change over time.

In sum, unconventional historical methods play a critical role in ecology, sometimes bolstering inferences made using other methods, but also frequently challenging such inferences.

Future directions in historical plant ecology—A key challenge in global change biology is reconciling the sometimes

Time lags in extinction and colonization may lead to erroneous conservation decisions. Imagine two forest patches in an otherwise stable but fragmented landscape. At time zero, one 10-ha patch is created on former agricultural land (initially devoid of forest species) while the second patch—a pre-existing forest remnant—is reduced from 10 ha to 5 ha. Assume equivalent growing conditions in the two patches and a constant rate of colonization from other patches in the landscape, which effectively constitute a “mainland”. We model the probability of patch occupancy using the mainland-island version of Levins (1969) metapopulation model: $dP/dt = c(1 - P) - eP$, where P is the probability of occupancy, c the colonization rate, and e the extinction rate. Equilibrium patch occupancy is $P_{eq} = c/(e + c)$. For heuristic purposes, we assume a large species pool of perennial forest plants, each of which obeys the same dynamics, such that P is equivalent to the proportion of the species pool present in a given patch (proportional species richness). For slow-dispersing forest plants in a fragmented landscape, $c = 0.01$ is a reasonable approximation (Vellend, 2004; Verheyen et al., 2004). If we assume e is inversely proportional to the square of area, corresponding to local populations with relatively low temporal fluctuations (Hanski, 1994), then a reduction of patch area by half corresponds to a 4-fold increase in e . Fig. 5 illustrates temporal dynamics for the two patches: (1) a new 10 ha patch with $c = 0.01$ and $e = 0.005$; (2) a patch that has been reduced in area from 10 ha to 5 ha ($c = 0.01$, $e = 0.02$). It takes many decades for the extinction debt to be paid in patch 1 and for the colonization credit to accrue in patch 2. Importantly, for more than 50 yr, the difference in species richness between the two patches is in the opposite direction compared to the difference once the time lags have ended ($P_{eq} = 0.33$ in patch 1 and 0.67 in patch 2), such that basing conservation decisions on observed species richness during this period (e.g., prioritizing patch 2 over patch 1) would be misguided.

Box 1. The importance of taking time lags into account in conservation assessment

contradictory results emerging from different methods of drawing inferences about cause and effect relationships. While studies using different approaches can be fruitfully compared post hoc, studies that explicitly integrate historical and contemporary methods can be especially valuable. For example, Herben et al. (2006) combined data on landscape change over the past 150 yr (using maps and photographs) with detailed contemporary demographic data on the grassland plant *Succisa pratensis* Moench to conclude that the present-day distribution of this species still reflects aspects of landscape structure in the 19th century. The novel insights revealed by this and other studies (e.g., Baeten et al. [2010] just described) indicate that there is tremendous scope for more research that explicitly integrates multiple sources of historical and contemporary data.

For some ecological questions and regions, the exploitation of unconventional historical data sources is only in its infancy. Of particular note is the use of such data sources in the tropics, where Feeley and colleagues have begun using herbarium specimens to model species distributions and responses

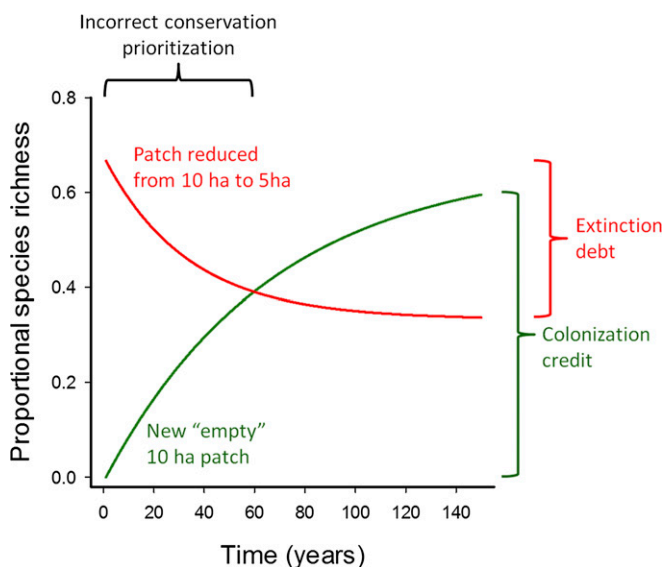


Fig. 5. Concurrent extinction debts and colonization credits in different patches in a fragmented landscape, illustrated using the mainland-island version of Levins' (1969) metapopulation model (see Box 1). The green line represents a new 10 ha forest patch with colonization rate, $c = 0.01$ and extinction rate, $e = 0.005$; the red line represents a patch that has been reduced in area from 10 ha to 5 ha ($c = 0.01$, $e = 0.02$).

to global change factors (Feeley and Silman, 2010, 2011; Feeley, 2012; see earlier discussion). Similarly, in a review of historic alpine flora surveys in Europe, Stöckli et al. (2011) found ~300 legacy studies that are suitable for resurveys to evaluate community compositional changes over time. Given the unique insights provided by such studies and the pressing need to understand the underpinnings of global biological change, continued historical sleuthing to locate and use such data sources should be an important research priority. The value of such data also serves as a reminder of the importance of continuing to collect and permanently archive tomorrow's historical data such as herbarium specimens, vegetation surveys, etc.

Historical data provide a long-term view of ecological change, but inferences about the causes of such change are necessarily indirect. Explicit predictions can be made based on different hypothesized drivers of change, and to date, many authors have been careful to evaluate competing predictions, such as those based on land use vs. climate (e.g., Bjorkman and Vellend, 2010; Harrison et al., 2010). However, there is always some risk that a high level of interest in some processes (e.g., climate change) can create tunnel vision among researchers, such that alternative explanations for observed patterns might not receive sufficient attention. For example, there is a large literature on the relationship between temperature and flowering phenology, but many other factors, such as timing of snow melt and precipitation, can also influence phenology (Pau et al., 2011; Iler et al., 2013, in this issue). Similarly, contemporary increases in the cover and abundance of shrub species in tundra ecosystems has been linked to ongoing climate warming (Elmendorf et al., 2012); however, the currently observed changes may also be due to continued shrub growth and clonal expansion following a recruitment pulse coincident with the end of the Little Ice Age (ca. 1850, Tape et al., 2006; Myers-Smith et al., 2011). In sum, while

certain drivers of vegetation change may be of particular interest, it is critically important to consider not only alternative hypotheses for the causes of temporal patterns but also interactions between processes operating on different temporal and spatial scales.

CONCLUSION

Ultimately, ecologists would like to predict the future responses of ecosystems to global change. As with models of climate change itself, a critical ingredient in our ability to predict forward is an understanding of changes that have occurred in the past. Historical ecological methods have and will continue to provide insights of fundamental importance, reshaping our understanding of plant responses to a rapidly changing world.

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